LEAF LIGHT REFLECTANCE, TRANSMITTANCE, ABSORPTANCE, AND OPTICAL AND GEOMETRICAL PARAMETERS FOR ELEVEN PLANT GENERA WITH DIFFERENT LEAF MESOPHYLL ARRANGEMENTS[1]

H. W. Gausman, W. A. Allen, C. L. Wiegand,

D. E. Escobar, and R. R. Rodriguez[2]

Southern Plains Branch
Soil and Water Conservation Research Division
Agricultural Research Service
U. S. Department of Agriculture
Weslaco, Texas

SUMMARY

Internal leaf structure differences among 11 plant genera are related to their spectrophotometrically measured light reflectance and transmittance and calculated absorptance values over the 500- to 2500-nanometer (nm) wavelength interval (WLI), to percent water content, and to leaf thickness measurements.

Leaf water contents ranged from 60% for isolateral (palisade layers on both sides) eucalyptus to 95% for succulent begonia leaves with storage cells on each side of a central chlorenchyma. Dorsiventral leaves (palisade upper, spongy parenchyma lower) had both high (95%) and low (60%) water contents.

Dorsiventral rose and compact corn leaves (no palisade cells) were thinnest (0.15 mm), and succulent sedum leaves were thickest (0.82 mm).

Eucalyptus, corn, and oleander had the highest correlation coefficients of -0.73, 0.64, and 0.64, respectively, between leaf thickness and water content.

Bottom leaf surfaces of dorsiventral leaves had higher reflectance values than top leaf surfaces, indicating that the spongy parenchyma contribute more to light scattering than the palisade parenchyma of the leaf mesophyll.

Thick oleander, crinum, ficus, sedum, and ligustrum leaves had the lowest light transmittance. Transmittance values were lower when light was passed from the top through the leaves compared with passing light from the bottom through the leaves. The difference in transmittance was caused by greater light diffusion by top leaf surfaces.

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[2] Plant Physiologist, Research Physicist, Research Soil Scientist, Biological Laboratory Technician, and Physical Science Aid, respectively, USDA, Weslaco, Texas 78596.

At the 550-nm wavelength (representing the 400- to 750-nm visible region), reflectance was greater from the bottom than from the top of dorsiventral leaves, indicating that the chloroplasts in the palisade cells absorbed light. Bottom and top reflectance values were the same for the compact corn leaves. Considering top leaf surfaces only, thick, succulent sedum and thick ficus leaves had the highest and lowest reflectance values of 20 and 8%, respectively.

Transmittance was lowest for ficus and highest for succulent begonia leaves. Compact leaves of corn and succulent leaves of sedum and begonia, tending to have a continuous mesophyll arrangement, had the lowest light absorptance of 70%. Thick dorsiventral leaves of ficus, oleander, and ligustrum with multiseriate epidermal layers or multipalisade layers had the highest light absorptance of 80 to 90%.

At the 1000-nm wavelength (representing the 750- to 1450-nm near-infrared region), reflectance values from top and bottom leaf surface measurements were essentially alike. Compact corn leaves had the lowest reflectance of 43% and succulent sedum and dorsiventral ficus, oleander, ligustrum, and crinum leaves had the highest reflectance of 53%. The 35.0% transmittance of oleander leaves was lowest, and the 54.5% for corn was highest. The thin corn and rose leaves had the lowest absorptance values of 2 to 3% and the thick leaves of ligustrum, ficus, crinum, sedum, and oleander had the highest values of 8 to 11%.

Coefficients of determination are briefly considered that accounted for at least 60% of variation between leaf thickness and reflectance; leaf thickness and absorptance; leaf water content and reflectance; and leaf water content and absorptance.

Experimental values of leaf reflectance and transmittance for the 11 genera have been transformed into effective optical constants that are useful in predicting reflectance phenomena associated with leaves either stacked in a spectrophotometer or arranged naturally in a plant canopy. The index of refraction n is plotted against wavelength to obtain dispersion curves. The absorption coefficient k is shown to be equivalent to values determined previously for leaves of agricultural crops.

Each of the 11 genera has been analyzed to obtain geometrical parameters that specify the amount of water and air in the leaf. The water parameter is the thickness of liquid water necessary to produce the observed leaf absorption. Observed and computed values of leaf water thickness have been obtained. Agreement is good except for ligustrum, crinum, and sedum. The air parameter is the number of identical compact layers into which the equivalent water must be subdivided in order to achieve the observed partition of light between reflectance and transmittance.

A third parameter, infinite reflectance, is observed when leaves are piled sufficiently deep. Infinite reflectance has been tabulated at the 1.65 μm (micrometer) wavelength for all 11 genera. Infinite reflectance is shown to be a function of the calculated thickness of the identical compact layers of which a leaf is assumed to be composed.

INTRODUCTION

To interpret data sensed from air or spacecraft or from radiation interactions within plant canopies and communities, interactions of different leaf structures (mesophyll arrangements) with electromagnetic radiation must be understood.

Although considerable literature empirically considers interaction of plant leaves with electromagnetic radiation, scant attention has been given to effects of internal structural differences (mesophyll arrangements) among leaves on spectral energy relations (Gausman et al., 1971). Shul'gin, Khazanov, and Kleshnin (1960) did relate light reflectance over the 400- to 800-nanometer (nm) wavelength interval (WLI) to leaf surface morphologies of many plant genera.

Their main interest, however, was the angular distribution of light scattered off leaf surfaces. Shiny xeromorphic leaves had maximum reflection at small angles (to 15 degrees), pubescent[3] leaves at 10 to 15° and 60 to 70°, and wrinkled and dull leaves at 70 to 80°. Howard (1966) studied spectral relations of eucalyptus leaves, that have an isolateral mesophyll arrangement (palisade parenchyma cells on both sides).

The hypothesis for the research reported here was that leaf mesophyll arrangements influence spectral energy measurements of leaves. Accordingly, differences in internal leaf structure among 11 plant genera have been compared with: (1) spectrophotometrically measured reflectance and transmittance and calculated absorptance values of the leaves over the 500- to 2500-nm WLI, (2) percent leaf water contents, (3) leaf thickness measurements, and (4) optical and geometrical leaf parameters.

MATERIALS AND METHODS

Eleven plant genera were selected primarily to provide differences in leaf mesophyll arrangements, and concurrently wide variations occurred in leaf thicknesses and water contents, and other structural parameters. Leaf characteristics of the 11 genera are described in Table 1, and typical leaf transections of 10 genera are portrayed in Fig. 1.

Ten full-grown and healthy-appearing leaves were harvested from each of the 11 plant genera. Immediately after excision, leaves were wrapped in Saran or Glad-Wrap[4] to limit dehydration. Leaves were wiped with a slightly dampened cloth to remove surface contaminants before spectrophotometric measurements.

Spectral diffuse reflectance and transmittance were measured on adaxial[5] (top) and abaxial (bottom) surfaces of single leaves over the 500- to 2500-nm WLI with a Beckman Model DK-2A spectrophotometer equipped with a reflectance attachment. Data have been corrected for decay of the MgO standard (Sanders and Middleton, 1953) to give absolute radiometric data.

Leaf thickness and diffuse reflectance and transmittance measurements and tissue fixation processing were completed within 6 hours after leaves were harvested for each genus.

Leaf thickness was measured with a linear displacement transducer and digital voltmeter (Heilman et al., 1968); area per leaf was determined with a planimeter, except that area per leaf of corn and crinum was calculated by the method of Slickter, Wearden, and Pauli (1961). Percent leaf water content was determined on an oven-dry weight basis by drying at 68°C for 72 hours and cooling in a desiccator before final weighing.

Tissue pieces, taken near the center of leaves approximately one-half inch on either side of the midrib, were fixed in formalin-acetic acid-alcohol (FAA), dehydrated with a tertiary butyl alcohol series, embedded in paraffin, stained with either the safranin-fast green or the safranin-fast green-orange G combinations (Jensen, 1962), and transversally microtomed at 12 or 14 μ (micron) thicknesses. The relatively thick transverse sections (12 to 14 μ) were used to accentuate the intercellular spaces, and thus enhance differences in mesophyll arrangements among the plant genera. Photomicrographs were obtained with a Zeiss Standard Universal Photomicroscope.

Variance and correlation (Steel and Torrie, 1960), and Duncan's multiple range test (Duncan, 1955) were used in the statistical analyses of the spectrophotometric data. Data given are averages of 10 leaves (replications).

RESULTS AND DISCUSSION

Full-grown leaves were used in this study because leaf maturation affects spectral energy relations, leaf water contents, and leaf thicknesses (Gausman et al., 1970).

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[3] Botanical terms are defined in the GLOSSARY OF TERMS.

[4] Trade and company names are for the convenience of the reader and do not imply an endorsement or preferential treatment by the U. S. Department of Agriculture.

[5] Although not technically correct, for simplicity top and bottom will be used henceforth in the text to denote adaxial and abaxial leaf surfaces, respectively.

The influence of leaf maturation on reflectance and transmittance is associated with compactness of internal cellular structure. Differences in cellular compactness of cotton leaves, sampled from fourth or fifth nodes down from plant apexes, affected reflectance of near-infrared light, 750 to 1350 nm (Gausman, Allen, and Cardenas, 1969a). Reflectance of older leaves was increased because of an increase in intercellular spaces or air voids (Willstätter and Stoll, 1918). Scattering of light within leaves occurs most frequently at cell wall (hydrated cellulose)- air cavity interfaces which have refractive indices of 1.4 and 1.0, respectively (Weber and Olson, 1967).

Very immature cells in young leaves are primarily protoplasmic with little vacuolate cell sap storage (Esau, 1965; Fahn, 1967; Lundegårdh, 1966). During cell growth (extension), cell water-filled vacuoles develop that usually coalesce to form a central sap cavity, and the protoplasm covers the cell wall in a thin layer. Hydrated leaves, compared with dehydrated leaves, reflected less and absorbed more light over the 500- to 2500-nm WLI (Allen and Richardson, 1968).

Leaf Water and Thickness

Percent leaf water contents, Fig. 2, ranged from 60% for eucalyptus to 95% for begonia and sedum leaves. Statistically (Duncan's multiple range test), leaves of hyacinth and banana, and leaves of begonia and sedum were alike in water content; all other genera differed significantly, $p = 0.01$. Succulent leaves represented by begonia and sedum were high in percent water content as expected, because of the presence of water-storing tissue (Fahn, 1967). There is no apparent association of leaf mesophyll arrangements, Fig. 1, with percent leaf water contents, Fig. 2.

Figure 3 depicts leaf thicknesses of the plant genera. Rose and corn leaves were thinnest (about 0.15 mm), and sedum leaves were thickest (about 0.82 mm). Statistically, six groups of genera alike in leaf thickness were: rose, corn, banana; banana, eucalpytus; hyacinth, oleander, begonia; oleander, begonia, ligustrum; ligustrum, ficus; and ficus, crinum. As with leaf water content, there is no apparent relation of leaf structure, Fig. 1, to leaf thickness, Fig. 3.

Eucalpytus, corn, and oleander had the highest correlation coefficients of -0.73, 0.64, and 0.64, respectively, between leaf thickness and water content. It is postulated that the negative correlation of eucalyptus is caused by contiguous columnar air spaces between the lower and upper epidermis among palisade cells of the isolateral leaf that develop with leaf maturation and facilitate vapor loss.

General Spectra of Leaves

The spectral range 500- to 2500-nm WLI can be characterized by three categories (Weber and Olson, 1967; Thomas, Wiegand, and Myers, 1967): (1) the visible region 500 to 750 nm, dominated by pigment absorption of light; (2) the near-infrared region 750 to 1350 nm, a region of high reflectance affected primarily by leaf structure; and (3) the interval 1350 to 2500 nm, a region greatly influenced by the amount of water in the tissue - strong water absorption bands occur at 1450 and 1950 nm.

Spectral data for top (adaxial) and bottom (abaxial) leaf surfaces of all genera for 550-, 800-, 1000-, 1450-, 1650-, 1950-, and 2200-nm wavelengths are given in Tables 2, 3, and 4. Although many comparisons could be made, one example will show the utility of the data. Considering the 1000-nm wavelength data for top leaf surfaces in Tables 2, 3, and 4, reflectance was highest for dorsiventral ligustrum, crinum, and oleander leaves and lowest for compact corn leaves; transmittance was lowest for oleander and highest for corn leaves; and absorptance for corn and oleander leaves was 2.8 and 11.0%, respectively. The relatively compact corn leaf with low light reflectance and high transmittance had fewer intercellular air spaces (air voids) than the dorsiventral oleander leaf.

Mean Spectral Values (Data not included)

Because the interaction of genera with wavelengths was small, mean spectral measurements of 550-, 800-, 1000-, 1450-, 1650-, 1950-, and 2200-nm wavelengths were compared. Bottom leaf surfaces of dorsiventral leaves had higher reflectance values than top leaf surfaces, indicating that the spongy parenchyma contribute more to light scattering than the palisade parenchyma of the leaf mesophyll. This was substantiated by equal reflectance values of top and bottom surfaces of compact corn leaves.

Thick leaves of oleander, crinum, ficus, sedum, and ligustrum had lowest percent transmittance. Mean spectrophotometrically measured transmittance values were lower when light was passed from the top through the leaves compared with passing light from the bottom through the leaves. The difference in transmittance was caused by greater light diffusion by top leaf surfaces. The

spectrophotometer used irradiates the specimen with direct light. There is no reason to expect, therefore, that transmittance would be independent of the direction of illumination as is the case for diffuse light.

Diffuse reflectance data were made absolute by correcting for decay of the MgO standard on the spectrophotometer (Sanders and Middleton, 1953), and absorptance was calculated as: 100 - [percent reflectance + percent transmittance]. When data for wavelength interval 500 to 2500 nm were averaged (data not shown), highest absorptance values of 60.6, 58.2, 59.1, and 58.3% were obtained for the thick, dorsiventral ficus, crinum, ligustrum, and oleander leaves, respectively; and lowest values of 40.4 and 39.0% were obtained for the thin, compact corn and thin, dorsiventral rose leaves, respectively.

550- and 1000-nm Wavelength

Intensive study was given to the 550- and 1000-nm wavelengths, representing the visible (400 to 750 nm) and near-infrared regions (750 to 1450 nm), respectively. At the 550-nm wavelength (Fig. 4), reflectance was greater from the bottom than from the top of dorsiventral leaves, indicating that the chloroplasts in the palisade cells absorbed light. Bottom and top reflectance values were the same for the compact corn leaves. Considering top leaf surfaces only, thick, succulent sedum leaves with the highest water content had the highest reflectance of 20%, and thick ficus leaves with a medium water content had the lowest reflectance of 8%.

Percent transmittance (Fig. 5) was lowest for ficus and highest for succulent begonia leaves. Compact leaves of corn and succulent leaves of sedum and begonia, tending to have a continuous mesophyll arrangement, had the lowest light absorptance of approximately 70% (Table 4). Thick dorsiventral leaves of ficus, oleander, and ligustrum with multiseriate epidermal layers or multipalisade layers had the highest light absorptance of 80 to 90%.

At the 1000-nm wavelength (Fig. 6), reflectance values from top and bottom leaf surface measurements were essentially alike. Compact corn leaves had the lowest reflectance of about 43% and succulent sedum and dorsiventral ficus, oleander, ligustrum, and crinum leaves had the highest reflectance of about 53%. The 35.0% transmittance of oleander leaves (Fig. 7) was lowest, and 54.5% for corn was highest. The thin corn and rose leaves had the lowest absorptance values of 2 to 3% (Table 4), and the thick leaves of ligustrum, ficus, crinum, sedum, and oleander had the highest values of 8 to 11%.

Correlations

Coefficients of determination were considered (data not shown) that accounted for at least 60% of variation between leaf thickness and reflectance; leaf thickness and absorptance; leaf water content and reflectance; and leaf water content and absorptance. Oleander, eucalyptus, and hyacinth leaves gave the highest correlation coefficients among the plant genera studied. In general, negative correlation coefficients were obtained between water content and reflectance and between thickness and reflectance measurements; and, with the main exception of eucalyptus, positive coefficients were obtained between leaf water content and absorptance and between thickness and absorptance calculations at 1450-, 1650-, 1950-, and 2200-nm wavelengths.

Optical Parameters

The flat-plate model (Allen et al., 1969) for calculation of effective optical constants of leaves was applied to the leaves of the 11 genera. All values of reflectance and transmittance for the leaves were reduced to average parameter values $\bar{a}$, $\bar{b}$ (Allen and Richardson, 1968) at the wavelengths 0.50, 0.55, ..., 2.50 μm. Thirteen data points in the vicinity of plant pigment and water absorption bands were deleted in advance (wavelengths 0.50, 0.55, 0.60, 0.65, 0.70, 1.40, 1.45, 1.50, 1.90, 1.95, 2.00, 2.45, and 2.50 μm) from calculations of refractive indices. This editing was justified because determination of n is weak in the vicinity of absorption bands.

Figures 8a, 8b, ..., 8k display the 95% confidence bands of the dispersion curves. Computational and statistical procedures used have appeared elsewhere (Freeze, 1964; Allen et al., 1970). Statistically, 95% of experimental points fall within the confidence limits. The dispersion curves of Fig. 8a, 8b, ..., 8k assumed to be cubics in wavelength λ, are expressed by the relation

$$n = \sum_i a_i \lambda^i \quad , \qquad (1)$$

where the coefficients a_0, ..., a_3 were determined by regression. Table 5 contains the coefficients of Eq. (1) for all data discussed.

Table 6 includes the leaf parameters that relate to the amount of water and air in the leaf.

The quantity D in the flat-plate model (Allen et al., 1969) is the equivalent thickness of liquid water necessary to produce the observed leaf absorption. The quantity N in the model is the number of compact layers into which D must be subdivided to achieve the observed partition of energy between reflectance and transmittance. The infinite reflectance R_∞ at the 1.65-μm wavelength (Allen and Richardson, 1968), produced by leaves piled sufficiently deep, is listed in column 5 of Table 6. The quantity R_∞ can be measured directly; the number listed in Table 6, however, is a calculated value obtained by techniques previously discussed (Allen and Richardson, 1968). The entries of Table 6 were obtained by adjusting the quantity D, over the spectral range 1.4 to 2.5 μm, to achieve the best fit of the leaf absorption k to the absorption k_o for liquid water. Column 6 of Table 6 is the quantity S.E. calculated from the relation

$$S.E. = \{\Sigma[\log (k/k_o)]^2/[n(n-1)]\}^{1/2} \qquad (2)$$

The summation in Eq. (2) includes the 23 values of 0.05-μm intervals over the 1.4- to 2.5-μm range. This quantity S.E. can be considered a figure of merit, because S.E. would vanish if the model was exact and the material was water. The quantities D and S.E. in Table 6 are positively correlated. This fact suggests that experimental difficulties begin to occur as the thickness of material is increased over the port of the spectrophotometer. As the specimen increases in thickness, lateral scattering losses begin. Such scattering losses appear as absorption losses in the bookkeeping. The effect is less in the region of the water absorption bands and greatest around the wavelengths 1.675 and 2.225 μm where more multiple reflections occur. The result is an increase in the valleys of the measured absorption curve and, consequently, a worse fit to the water data.

As indicated previously (Allen et al., 1970), the quantities D/N and R_∞ are strongly correlated. Figure 9 indicates the relationship. The quantity D and the leaf thickness are also correlated with R_∞. The thinner the leaf, the greater will be reflectance produced by a pile of such leaves. This fact has important implications in the interpretation of remote sensing data.

Table 7 is a compilation of the mean absorption spectra in cm^{-1} units over the range 1.4 - 2.5 μm of the 11 kinds of plant leaves. These values correlate (r = 0.997) with those previously obtained (Allen et al., 1970) on leaves of agricultural interest. The published values for liquid water are also presented in Table 7 for comparison. Figure 10 is a comparison of experimental and computed values of leaf water thickness obtained by procedures previously discussed (Gausman et al., 1970). Agreement is remarkably good except for the cases of ligustrum, crinum, and sedum. In the case of crinum the experimental value is greater, while in the cases of ligustrum and sedum the theoretical values are greater. The discrepancies must be attributed to failure of the flat-plate model to describe these leaves.

PROSPECTUS

Research of the type summarized here has been extended to 20 crop genera. We think results will be useful in investigations of light interactions in crop plant canopies. For example, infinite reflectance, R_∞, is one of the most promising of these quantities for crop discrimination procedures in remote sensing (Wiegand et al., 1969). Crop reflectance against dark soil background increases as numbers of leaf layers increase within a plant canopy until a stable reflectance value R_∞ is reached. In the 500- to 750-, 750- to 1350-, and 1350- to 2500-nm WLI, leaf area indices (LAI) of 2, 8, and 2 are required to reach R_∞, respectively. For example, a typical mature cotton leaf (Fig. 1) reflects about 48% of the incident light in the 750- to 1350-nm WLI, and transmits about the same amount of light to leaves below it on the plant, that, in turn, reflect about half and transmit about half of the light. Multiple transmission and reflection from leaves in a plant canopy result in an approximate 75% reflectance of incident light in the 750- to 1350-nm WLI. Thus, discrimination procedures using measurements of reflectance from space show considerable promise.

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Table 1.--Leaf mesophyll arrangement and other structural characteristics of plant leaves used in this study. Common names are used in the text.

Common name[6]	Latin name[7]	Mesophyll arrangement	Additional structural characteristics[8]
Corn	*Zea mays* L.	Compact	Bulliform cells on adaxial surface.
Banana	*Musa acuminata* Colla (*M. cavendishii* Lamb.)	Dorsiventral	Adaxial and abaxial hypodermal layers, palisade layer.
Begonia	*Begonia cucullata* Willd. (*B. semperflorens* Link & Otto)	Succulent, central chlorenchyma	Malacophyllous-type xerophytic leaf; large thin-walled storage cells on each side of central chlorenchyma.
Eucalyptus	*Eucalyptus camaldulensis* Dehnh. (*E. rostrata* Schlecht.)	Isolateral	Thick adaxial cuticle; no spongy parenchyma cells.
Rose	*Rosa* var. unknown	Dorsiventral	Multiple palisade layers.
Hyacinth	*Eichhornia crassipes* (Mart.) Solms	Dorsiventral	Multiple palisade layers; large air chambers characteristic of hydrophytes.
Sedum	*Sedum spectabile* Boreau	Succulent	Well-differentiated cellular structure.
Ficus	*Ficus elastica* Roxb. ex Hornem.	Dorsiventral	Thick adaxial cuticle; multiseriate adaxial epidermis; and multiple palisade layer.
Oleander	*Nerium oleander* L.	Dorsiventral	Thick adaxial cuticle; multiseriate epidermis; multiple palisade layer abaxial grooves.
Ligustrum	*Ligustrum lucidum* Ait.	Dorsiventral	Thick adaxial cuticle; multiple palisade layer.
Crinum	*Crinum fimbriatulum* Baker	Dorsiventral	Poorly differentiated and lobed palisade parenchyma cells; large central air spaces.

[6] Generic names used as common names are not italicized or capitalized in the text.

[7] Names are those used by New Crops Research Branch (Dr. Edward E. Terrell), ARS, USDA, Beltsville, Maryland 20705.

[8] Definitions are given in the GLOSSARY OF TERMS.

Table 2.--Percent diffuse reflectance of top (T) and bottom (B) leaf surfaces of 11 plant genera at seven wavelengths (nm).

Plant	550 nm		800 nm		1000 nm		1450 nm		1650 nm		1950 nm		2200 nm	
genera	T	B	T	B	T	B	T	B	T	B	T	B	T	B
Ficus	8.1	19.2	54.2	54.1	52.4	53.1	7.8	17.2	27.0	34.4	3.7	7.2	10.2	20.6
Ligustrum	10.2	26.9	55.5	53.8	54.1	53.4	9.0	20.8	27.7	37.7	4.1	8.7	11.1	24.2
Rose	10.4	20.5	48.8	43.2	48.4	42.6	23.2	24.6	38.0	34.6	9.4	13.8	25.1	25.8
Banana	10.5	16.9	44.0	41.3	43.3	40.7	12.0	15.9	29.0	29.4	5.1	8.2	16.0	19.0
Oleander	10.7	18.1	54.3	53.0	54.0	52.9	13.0	20.1	32.8	37.1	5.5	9.1	16.1	23.4
Hyacinth	12.1	19.0	49.8	49.4	49.6	49.1	11.7	18.4	31.0	34.8	4.8	8.2	15.3	21.9
Eucalyptus	12.6	15.8	45.9	46.0	45.4	45.6	16.0	18.2	29.7	31.0	7.0	8.3	15.6	17.6
Begonia	12.9	20.1	45.3	39.9	43.4	38.2	6.2	9.5	21.6	21.6	3.8	4.4	8.4	11.1
Corn	15.4	15.6	42.6	43.9	42.4	43.2	17.2	19.1	31.6	32.8	7.2	8.5	19.6	21.1
Crinum	15.6	23.1	55.8	54.6	54.1	53.2	10.0	14.8	29.3	33.4	5.2	6.8	13.6	19.4
Sedum	20.1	27.1	54.2	52.2	50.9	50.0	5.2	10.1	18.4	26.1	3.2	4.2	6.2	12.8

Table 3.--Percent transmittance of top (T) and bottom (B) leaf surfaces of 11 plant genera at seven wavelengths (nm).

Plant	550 nm		800 nm		1000 nm		1450 nm		1650 nm		1950 nm		2200 nm	
genera	T	B	T	B	T	B	T	B	T	B	T	B	T	B
Ficus	1.2	1.5	40.1	41.5	39.8	41.2	2.8	2.8	20.6	21.2	.5	.5	6.6	6.9
Ligustrum	3.9	3.9	38.1	40.1	38.4	40.0	4.2	4.4	21.4	22.0	.5	.5	8.2	8.4
Rose	9.3	11.2	48.6	54.1	49.5	55.2	27.1	31.1	44.1	49.3	10.9	13.0	33.8	38.1
Banana	12.2	13.2	52.1	54.8	52.5	55.4	17.1	18.5	41.4	43.8	2.6	2.9	26.9	28.6
Oleander	1.6	1.8	34.1	35.8	35.0	36.8	4.4	4.7	20.9	21.8	.5	.5	8.4	8.8
Hyacinth	8.5	8.8	45.2	47.0	45.9	47.6	9.1	10.2	31.6	33.6	.7	.9	16.6	18.4
Eucalyptus	7.5	7.3	48.3	48.3	49.8	49.8	17.9	18.2	36.2	34.2	3.8	3.8	22.4	22.3
Begonia	15.5	21.0	51.7	56.6	51.4	56.3	6.4	7.6	31.6	36.9	.5	.5	13.9	16.4
Corn	12.9	12.6	53.1	52.6	54.3	54.0	26.2	25.8	48.1	47.7	8.3	8.2	36.5	35.9
Crinum	6.1	6.6	38.1	39.4	37.7	38.8	1.9	2.1	18.5	19.2	.5	.5	6.2	6.4
Sedum	10.2	10.9	42.6	44.2	40.3	42.1	.5	.6	14.7	15.6	.5	.5	3.0	3.3

Table 4.--Percent absorptance, 100 - [% transmittance + % reflectance], of top (T) and bottom (B) leaf surfaces of 11 plant genera at seven wavelengths.

Plant	550 nm		800 nm		1000 nm		1450 nm		1650 nm		1950 nm		2200 nm	
genera	T	B	T	B	T	B	T	B	T	B	T	B	T	B
Ficus	90.5	79.3	5.7	4.4	7.6	5.8	89.3	79.9	52.4	44.2	95.8	92.2	83.1	72.4
Ligustrum	85.8	69.2	6.4	6.1	7.6	6.6	86.8	74.6	50.8	40.2	95.4	90.8	80.6	67.3
Rose	80.2	68.3	2.6	2.7	2.0	2.2	49.6	44.3	17.9	16.1	79.6	73.1	41.1	36.0
Banana	77.3	69.8	3.8	3.8	4.1	3.9	70.9	65.5	29.6	26.7	92.3	88.8	58.0	52.4
Oleander	87.8	80.1	11.6	11.3	11.0	10.3	82.6	75.2	46.3	41.0	94.0	90.4	75.4	67.8
Hyacinth	79.4	72.2	4.9	3.6	4.4	3.2	79.2	72.4	37.3	31.6	94.5	90.8	68.0	59.7
Eucalyptus	79.8	76.8	5.8	5.6	4.8	4.6	66.1	63.5	34.0	30.6	89.1	87.8	62.0	60.1
Begonia	71.6	59.0	2.9	3.4	5.2	5.5	87.4	82.8	46.6	42.5	95.6	95.1	77.6	72.4
Corn	71.5	71.8	4.2	3.4	2.8	2.7	56.5	55.0	20.2	19.5	84.4	83.2	43.8	43.0
Crinum	78.2	70.3	6.0	6.2	8.2	7.8	88.1	83.0	52.2	47.3	94.2	92.6	80.2	74.1
Sedum	69.6	62.0	3.2	3.6	8.7	7.8	94.2	89.3	66.8	58.2	96.2	95.2	90.8	83.8

Table 5.--Coefficients of dispersion curve $n = \Sigma a_i \lambda^i$ for leaves of 11 plant genera, where λ is expressed in micrometers.

Species	a_0	a_1	a_2	a_3
Eucalyptus	1.505	-.174	.038	-.005
Bananas	1.376	.072	-.098	.017
Rose	1.356	.109	-.125	.023
Ligustrum	1.323	.251	-.262	.054
Ficus	1.506	-.248	.144	-.035
Oleander	1.402	.036	-.082	.015
Crinum	1.417	.005	-.065	.008
Begonia	1.483	-.155	.058	-.021
Hyacinth	1.390	.028	-.056	.004
Corn	1.493	-.170	.054	-.013
Sedum	1.400	.016	-.051	-.000

Table 6.--Parameters that specify amount of water and intercellular air spaces in 11 kinds of plant leaves. Table headings are defined elsewhere[a].

Species	D(μm)	N	D/N	R_{∞}(%)[b]	S.E.
Eucalyptus	227	1.48	152	35.5	.022
Bananas	235	1.33	175	35.8	.012
Rose	116	1.59	72	49.9	.018
Ligustrum	515	2.24	229	29.0	.019
Ficus	593	2.09	283	27.2	.018
Oleander	421	2.38	176	34.3	.017
Crinum	532	2.27	233	30.4	.018
Begonia	496	1.36	362	24.1	.014
Hyacinth	329	1.76	186	35.0	.013
Corn	143	1.27	112	43.1	.014
Sedum	996	2.00	498	18.7	.027

a Allen, Gausman, and Richardson (1970).

b At 1.65-μm wavelength.

Table 7. Mean[a] absorption spectra in cm^{-1} units over the range 1.4 - 2.5 μm of the 11 kinds of plant leaves compared with published values for liquid water[b].

Wavelength (μm)	Leaf	Water
1.40	14.9 ± 1.9	12.5
1.45	25.7 ± 2.5	25.8
1.50	16.9 ± 1.5	18.5
1.55	9.6 ± 0.3	9.8
1.60	6.6 ± 0.3	6.5
1.65	5.4 ± 0.3	5.1
1.70	5.6 ± 0.5	5.2
1.75	7.1 ± 0.3	6.0
1.80	7.96 ± 0.3	8.1
1.85	13.96 ± 1.3	9.8
1.90	62.8 ± 11.9	81.0
1.95	75.1 ± 12.3	106.0
2.00	49.3 ± 6.8	68.0
2.05	33.6 ± 1.7	43.0
2.10	24.3 ± 1.2	26.0
2.15	19.3 ± 1.1	19.0
2.20	17.4 ± 1.0	16.0
2.25	20.3 ± 1.3	18.0
2.30	26.6 ± 1.5	22.0
2.35	34.7 ± 1.8	31.0
2.40	45.8 ± 4.8	43.0
2.45	57.2 ± 9.3	60.0
2.50	66.1 ± 8.8	83.0

a Each kind of leaf was assigned a statistical weight of unity.

b Curcio and Petty, 1951.

GLOSSARY OF TERMS

Esau (1965) and Fahn (1967) were used as sources for the definitions below.

Abaxial	Directed outwards from the axis (leaf surface faces away from the stem).
Adaxial	Directed toward the axis (leaf surface faces toward stem).
Chlorenchyma	Chloroplast - containing parenchyma tissue as the mesophyll and other tissues.
Compact leaf	Leaf, as corn (*Zea mays* L.), with a mesophyll comprised of relatively compact chlorenchyma with few intercellular spaces.
Cuticle	A layer of fatty substance, cutin, on the epidermal outer cell walls that is almost impermeable to water.
Dorsiventral leaf	A leaf with palisade parenchyma on one side of the blade, and spongy parenchyma on the other.
Epidermis	Primary in origin; if multiseriate (multiple epidermis) only the outer layer differentiates epidermal characteristics.
Groove	Stomatal crypt or epidermal depression found on the dorsal surface of oleander (*Nerium oleander* L.).
Hypodermis	Layer or layers of cells beneath the epidermis.
Intercellular space	Space among cells within the leaf.
Isolateral leaf	A leaf having palisade parenchyma cells on both sides of the blade.
Lysigenous space	An intercellular space that originated by cell dissolutions.
Lacuna (pl. lacunae)	Air space.
Mesophyll	Parenchyma tissue of a leaf between the epidermal layers.
Multiseriate	Consisting of many layers of cells.
Palisade parenchyma	Leaf - mesophyll parenchyma cells of elongated form perpendicular to the leaf surface.
Paradermal (tangential)	Refers to section made parallel with the surface of a leaf.
Parenchyma cell	Thin-walled cells capable of growth and division; found in leaves between the lower and upper epidermis.
Pubescent	Covered with hairs.
Sclerenchyma	Thick-walled cells whose principal function is strengthening (elements) of mature plant parts. Sclerenchyma cells may or may not have a protoplast at maturity.
Silica cell	Cell with silica within the cell wall.
Spongy parenchyma	Mesophyll parenchyma with conspicuous intercellular spaces.
Stoma	A pore in the epidermis and the two guard cells surrounding it. Sometimes stoma is applied to the pore only.
Storage cells	Large thin-walled cells used for storage of water and mucilages.
Succulent leaf	Fleshy-type leaves (malacophyllous) with many cells that store water and mucilages. Pertains to begonia (*Begonia cucullata* Willd.) with a central chlorenchyma and sedum (*Sedum spectabile* Boreau) with a continuous mesophyll of large thin-walled cells.

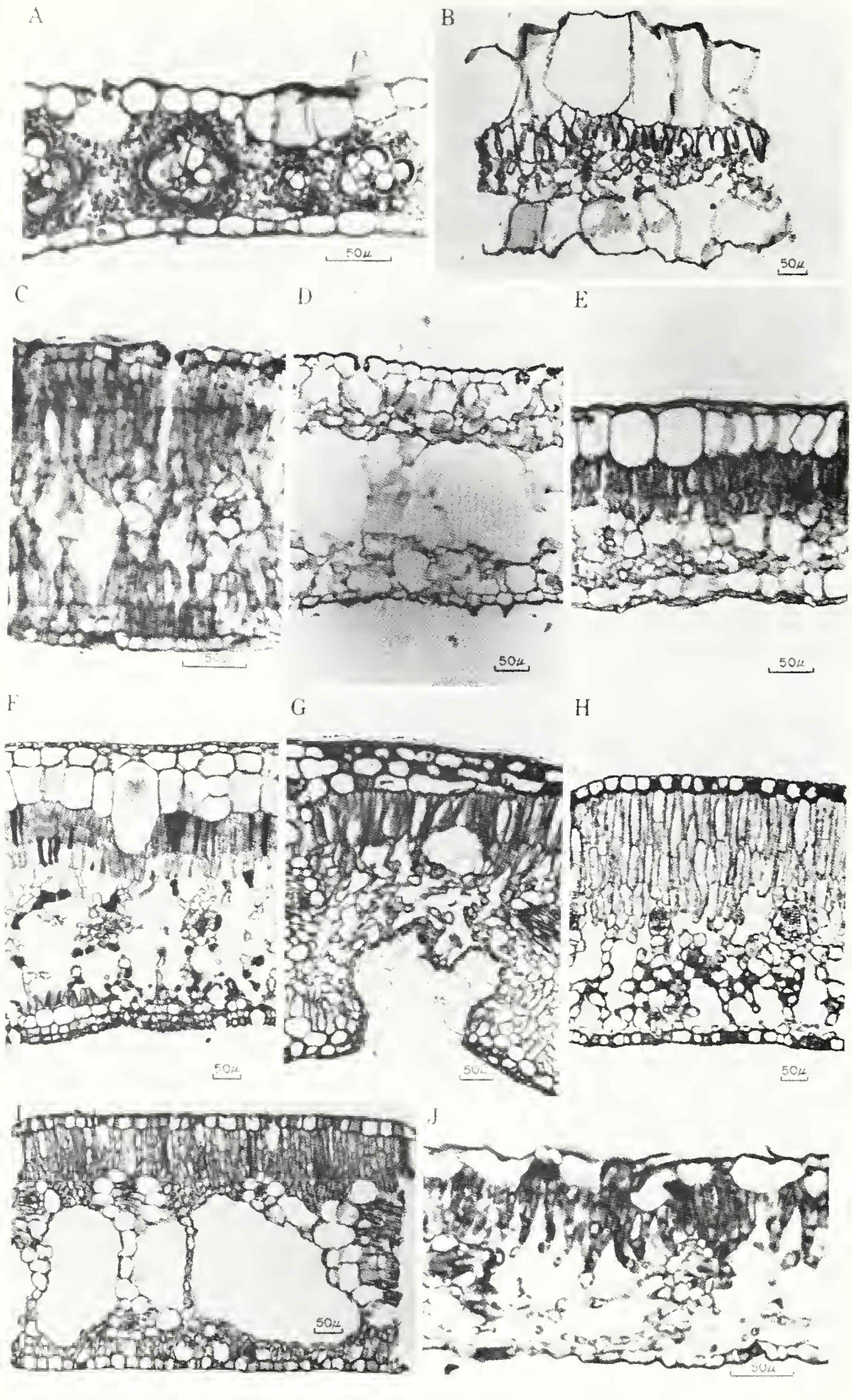

Figure 1. Photomicrographs of transections of 10 plant genera showing relative differences in leaf thicknesses, mesophyll arrangement, and other gross structural characteristics; A = corn (220 X), B = begonia (88 X), C = eucalyptus (220 X), D = crinum (88 X), E = banana (141 X), F = ficus (88 X), G = oleander (112 X), H = ligustrum (88 X), I = hyacinth (88 X), and J = rose (220 X). Sedum, a succulent leaf, was not included to lend symmetry to the photograph.

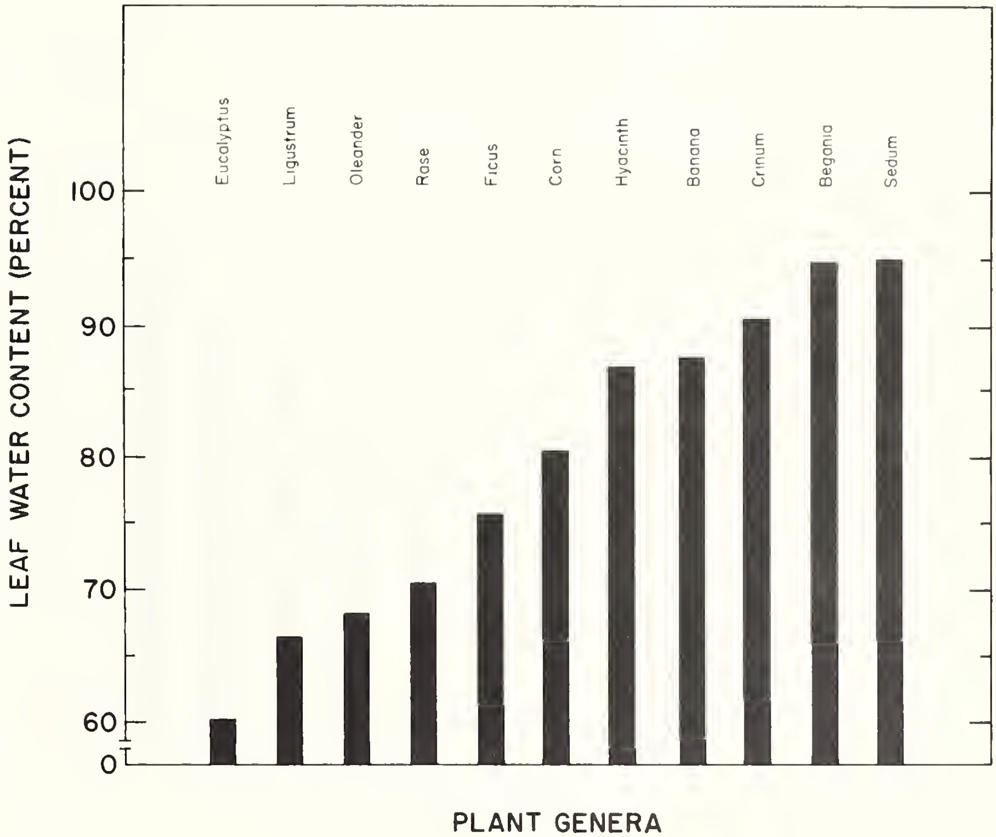

Figure 2. Percent leaf water contents (oven-dry weight basis) of 11 plant genera arranged in ascending order of water contents. Percent leaf water contents ranged from approximately 60% for isolateral (palisade layers on both sides) eucalyptus to 95% for succulent begonia and sedum leaves.

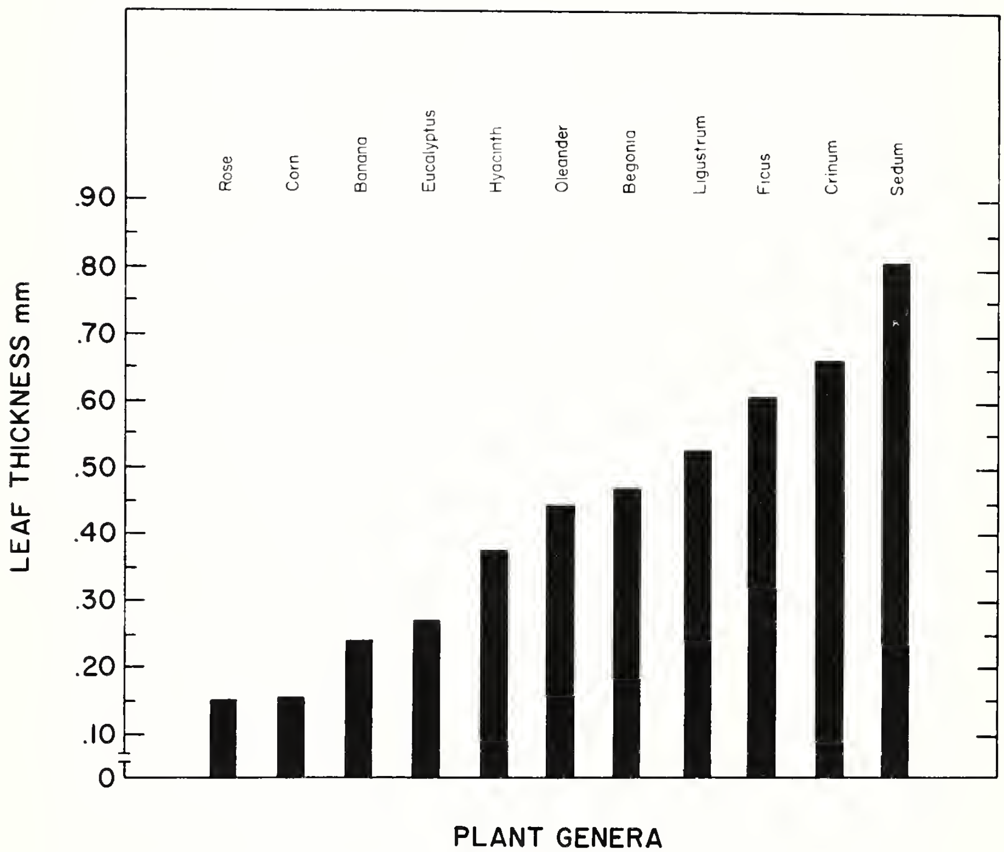

Figure 3. Leaf thicknesses of 11 plant genera arranged in ascending order of thickness. Dorsiventral rose leaves (palisade upper, spongy parenchyma lower) and compact corn leaves (no palisade cells) were thinnest, and succulent sedum leaves were thickest.

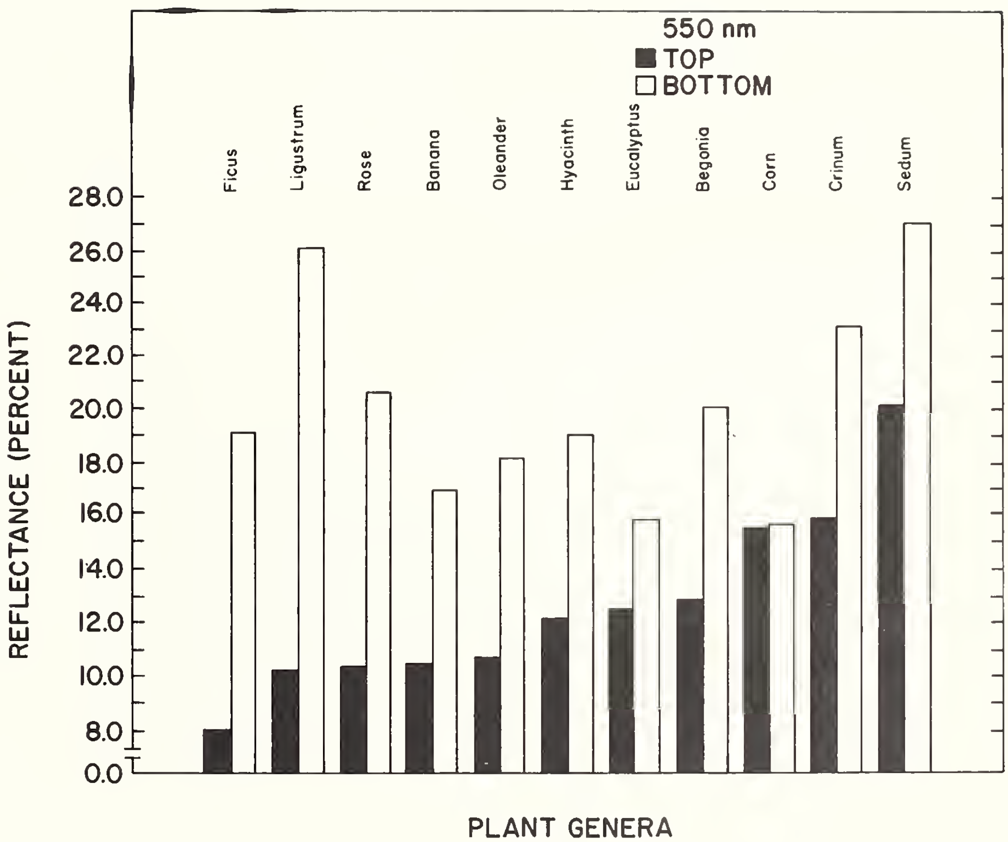

Figure 4. Reflectance of leaves of 11 plant genera at the 550-nm wavelength of top (adaxial) and bottom (abaxial) leaf surfaces. Bars are arranged in ascending order of reflectance for top leaf measurements. Reflectance was greater from the bottom than from the top of dorsiventral leaves such as ficus and ligustrum (palisade upper, spongy parenchyma lower) indicating that chloroplasts in the palisade cells absorbed light. Bottom and top reflectance values were the same for the compact corn leaves (no palisade cells).

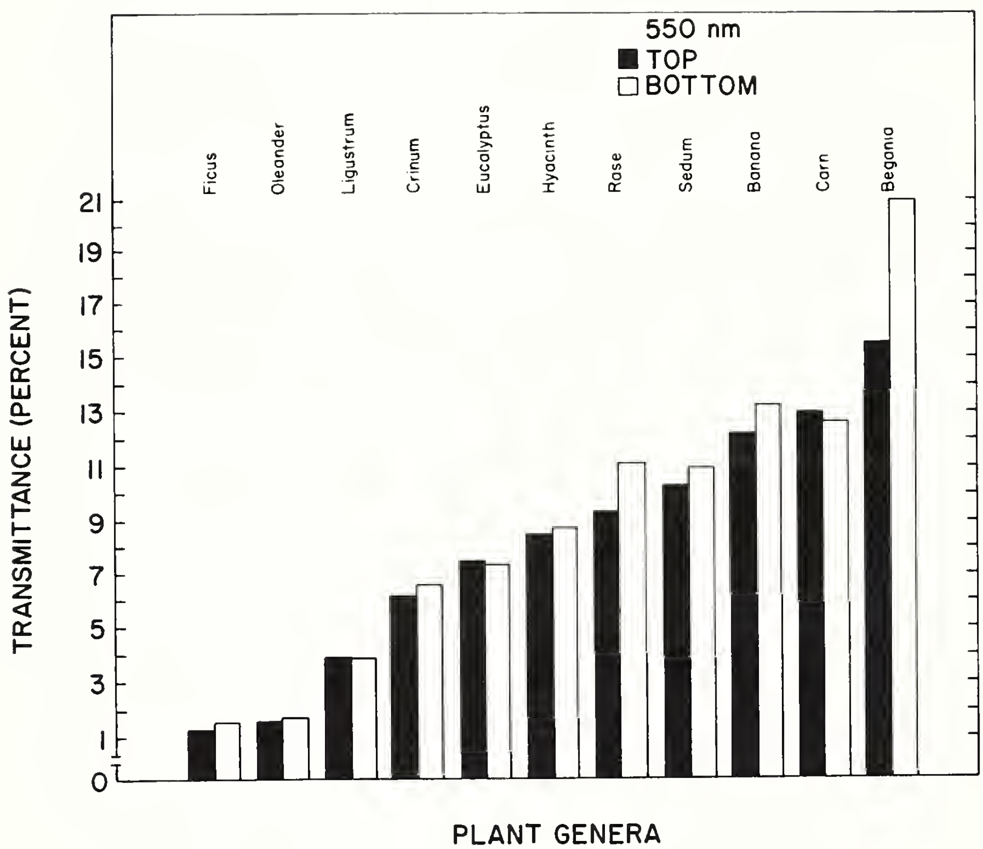

Figure 5. Transmittance of leaves of 11 plant genera at the 550-nm wavelength of top (adaxial) and bottom (abaxial) leaf surfaces. Bars are arranged in ascending order of transmittance for top leaf measurements. Percent transmittance was lowest for dorsiventral ficus and oleander leaves (palisade upper, spongy parenchyma lower) and highest for succulent begonia leaves.

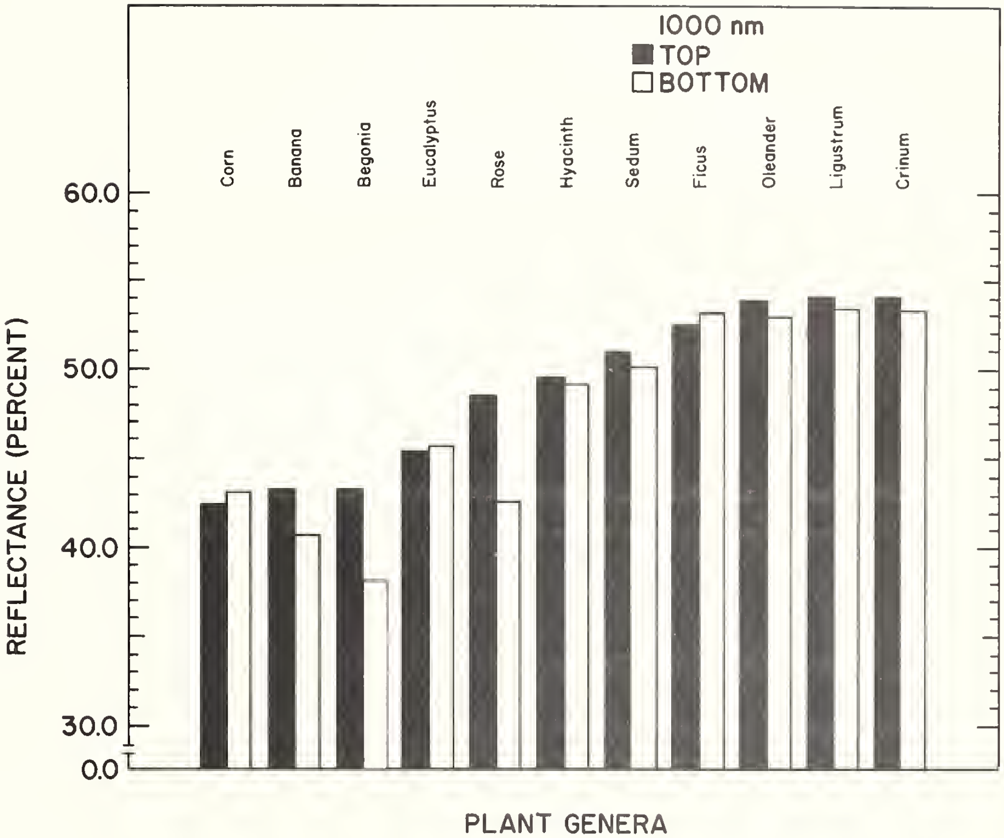

Figure 6. Reflectance of leaves of 11 plant genera at the 1000-nm wavelength of top (adaxial) and bottom (abaxial) leaf surfaces. Bars are arranged in ascending order of reflectance for top leaf measurements. Considering top leaf surfaces, compact corn leaves had the lowest reflectance and succulent sedum and dorsiventral (palisade upper, spongy parenchyma lower) ficus, oleander, ligustrum, and crinum leaves had the highest reflectance.

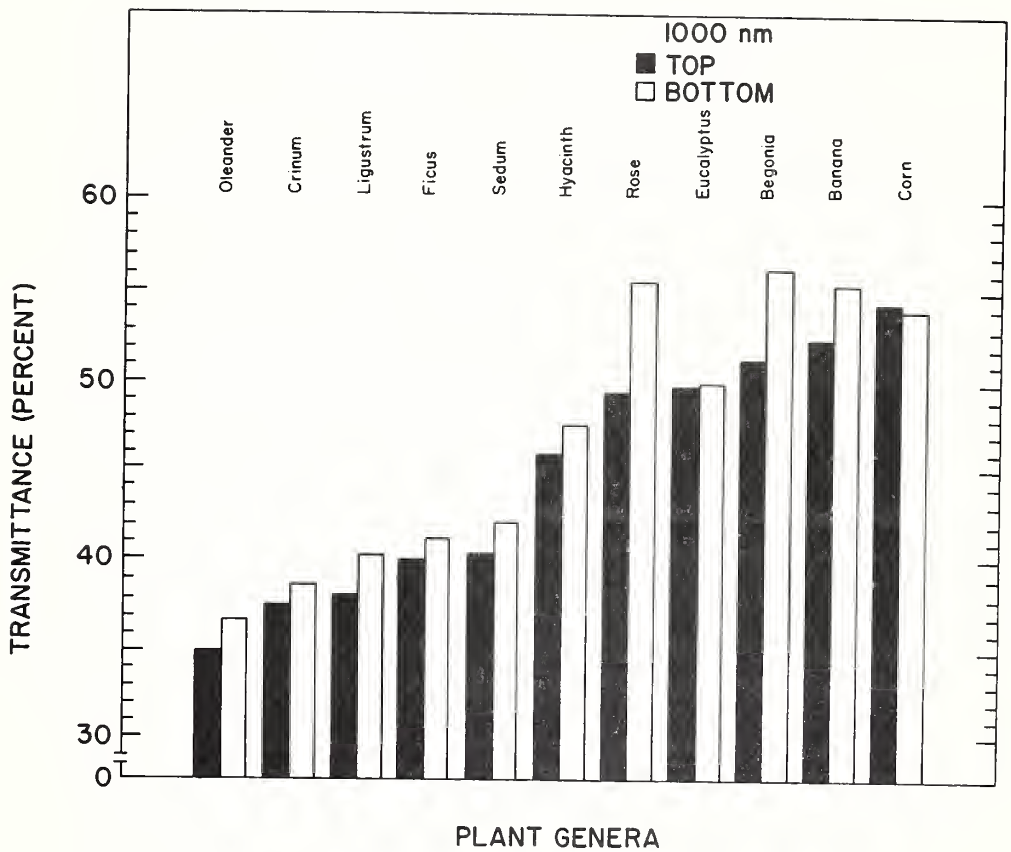

Figure 7. Transmittance of leaves of 11 plant genera at the 1000-nm wavelength of top (adaxial) and bottom (abaxial) leaf surfaces. Bars are arranged in ascending order for transmittance for top leaf measurements. Considering top leaf surfaces, dorsiventral oleander leaves (palisade upper, spongy parenchyma lower) had the lowest transmittance, and compact corn leaves had the highest transmittance.

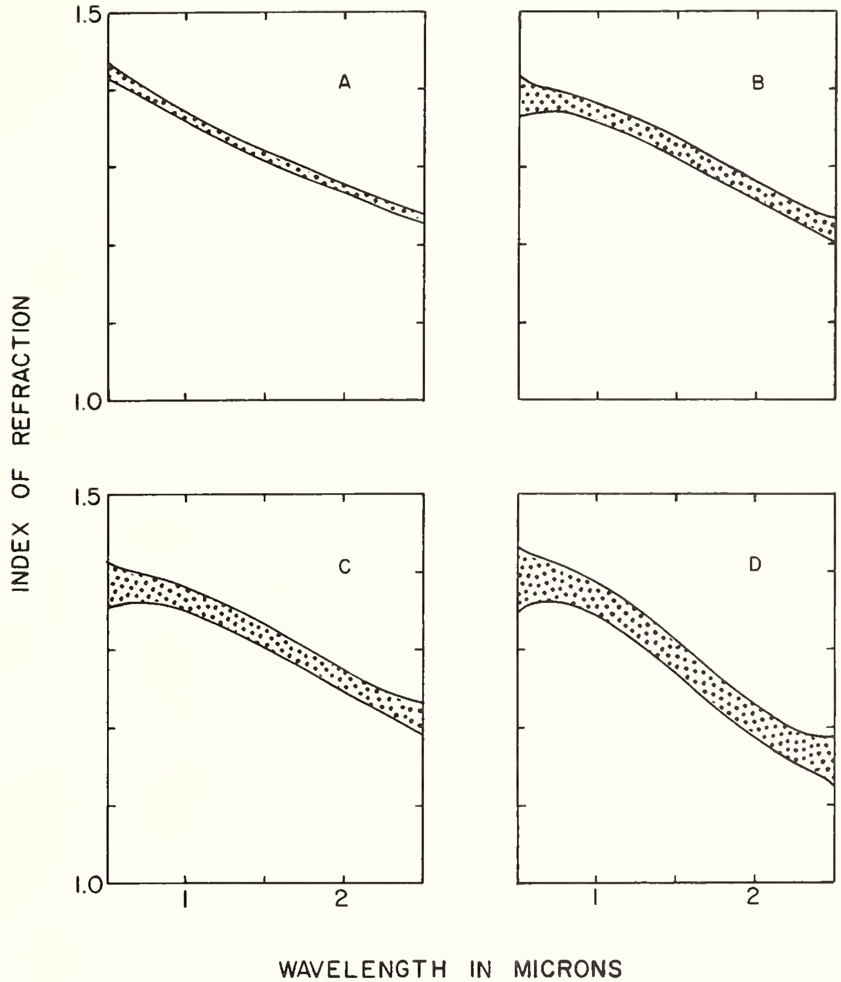

Figure 8. Dispersion curves for (A) corn; (B) banana; (C) begonia; (D) eucalyptus; (E) rose; (F) hyacinth; (G) sedum; (H) ficus; (I) oleander; (J) ligustrum, and (K) crinum. Figures 8A, 8B, ..., 8K display the 95% confidence bands of the dispersion curves. Statistically, 95% of experimental points fall within the confidence limits. The coefficients of the dispersion curves are shown in Table 5.

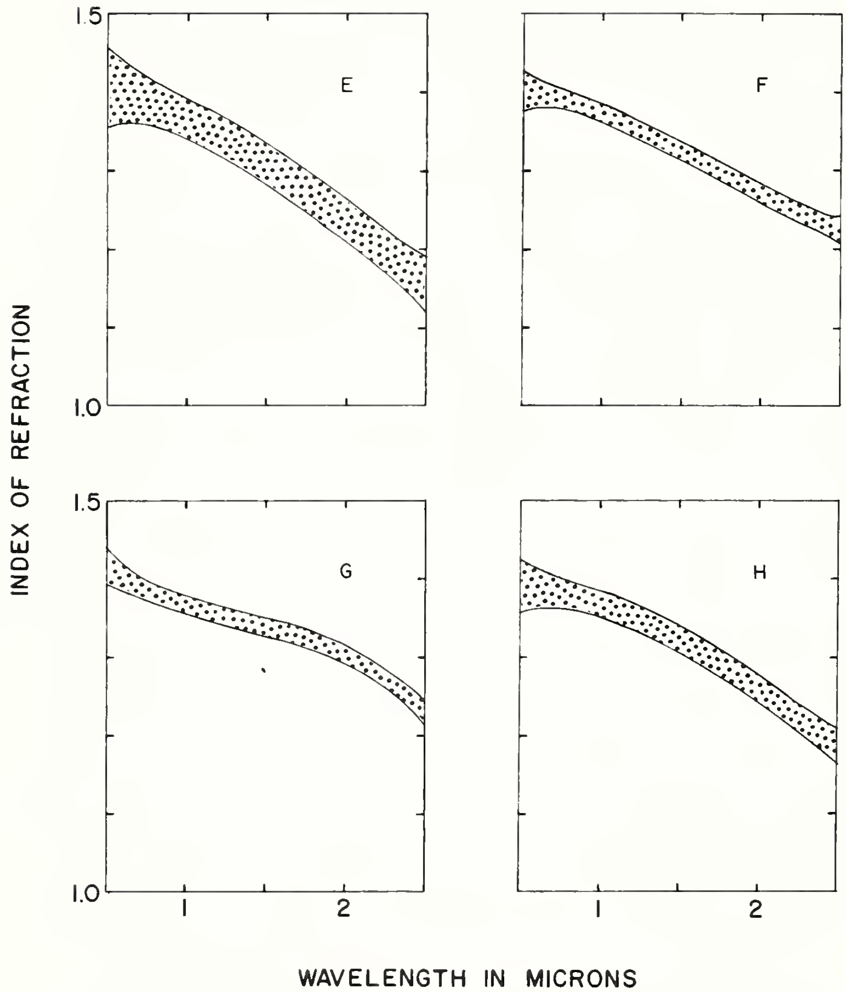

Figure 8. Continuation.

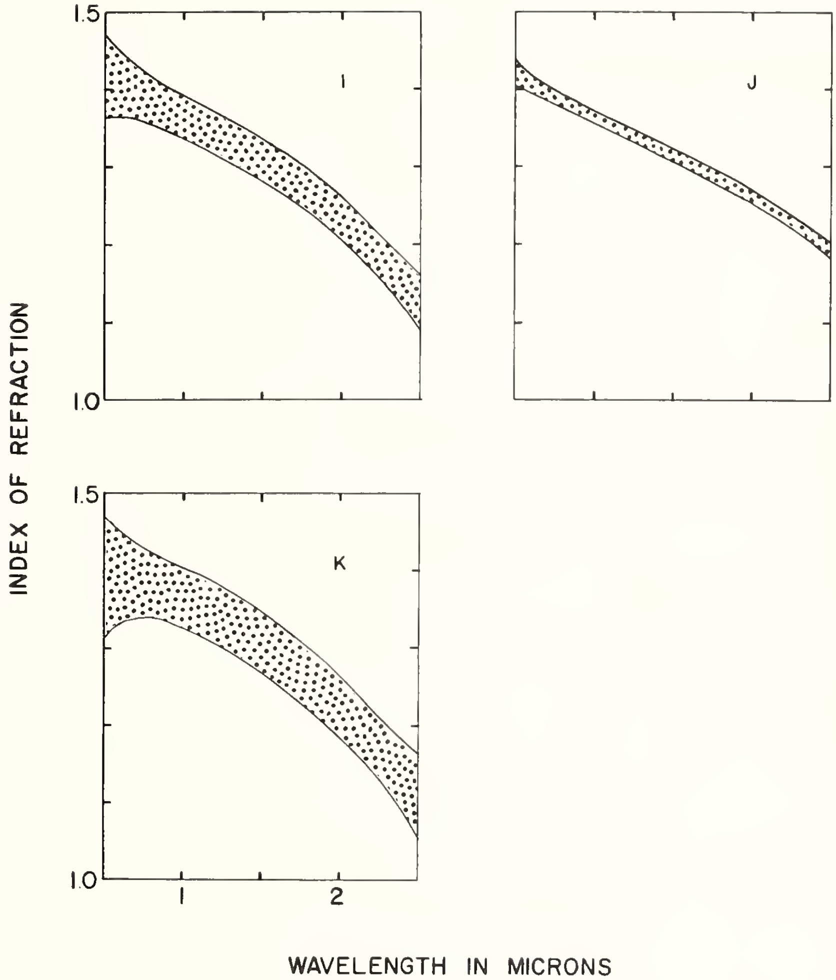

Figure 8. Continuation.

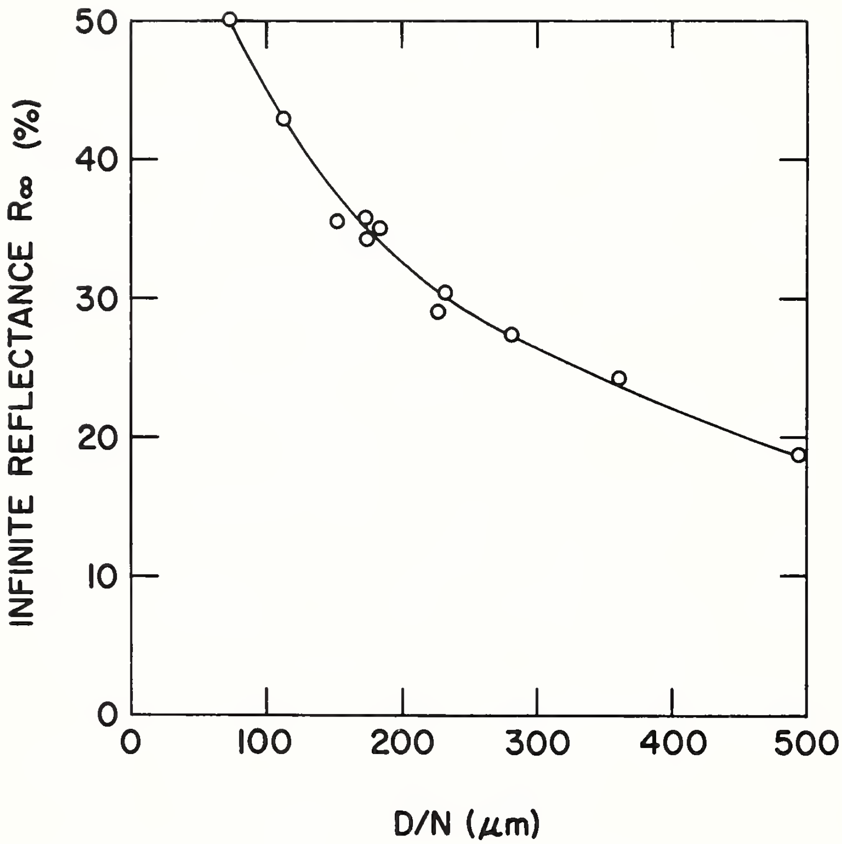

Figure 9. Infinite reflectance R_∞ at 1.65 μm for leaves of 11 plant genera plotted as function of characteristic linear dimension D/N, indicating that the quantities D/N and R_∞ are strongly correlated. The quantity D is the equivalent thickness of liquid water necessary to produce an observed leaf absorption, and N is the number of compact layers that D must be subdivided into to achieve an observed partition of energy between reflectance and transmittance.

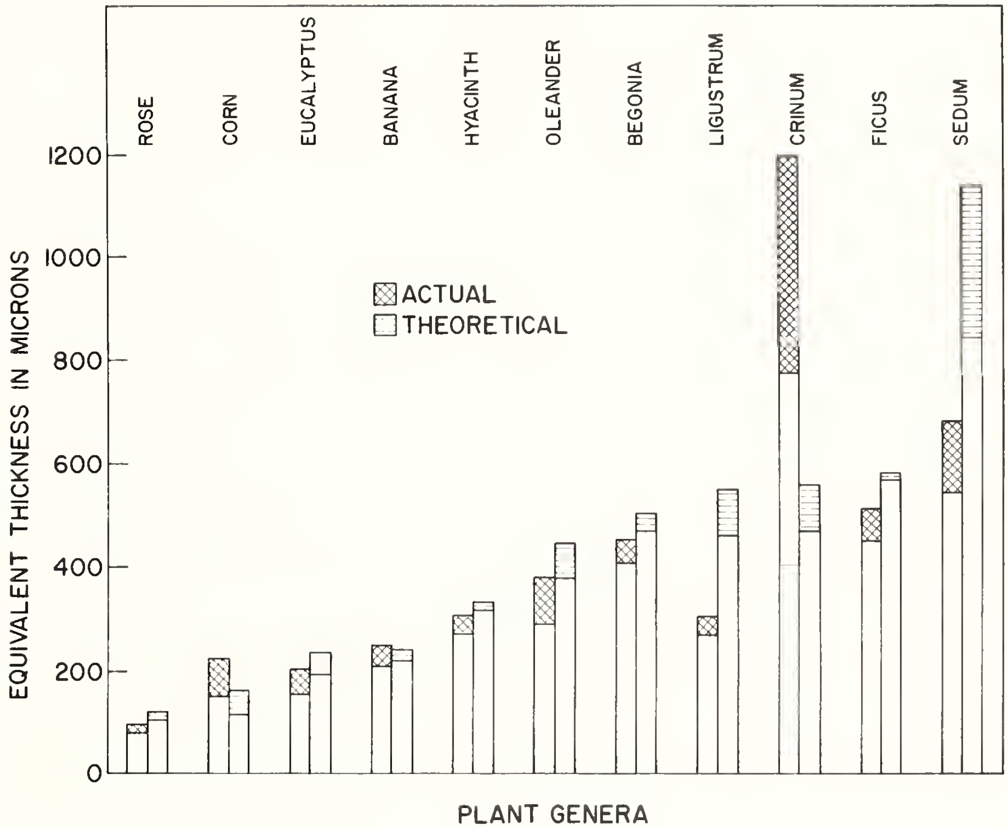

Figure 10. Comparison of observed and computed values of effective water thickness of leaves. The shaded areas represent variation of one standard deviation. Agreement between observed and computed values is remarkably good except for the cases of ligustrum, crinum, and sedum. In the case of crinum the experimental value is greater, while in the case of ligustrum and sedum the theoretical values are greater.